

Invasive ants reduce nesting success of an endangered Hawaiian yellow-faced bee, *Hylaeus anthracinus*

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Abstract

Hawaii has a single group of native bees belonging to the genus *Hylaeus* (Hymenoptera: Colletidae) and known collectively as Hawaiian yellow-faced bees. The majority of the 63 species have experienced significant declines in range and population. In 2016, seven species received federal protection under the Endangered Species Act of 1973. Competitors and predators, such as invasive bees, wasps and ants, are thought to be important drivers of range reductions and population declines, especially at lower elevations where more non-native species occur. We evaluated the effects of invasive ants on nesting *Hylaeus anthracinus* using artificial nest blocks that allowed us to track nest construction and development. The blocks were placed in pairs at 22 points encompassing three sites on the north and east sides of Oahu. One block in each pair was treated with a sticky barrier to prevent access by ants, while the other block remained untreated. From December 2015 to December 2016, we monitored 961 individual nests in the blocks. Seventy percent of nests in control blocks were invaded by ants. Nests in treated blocks were more likely to produce at least one adult than nests in untreated blocks (38% vs. 14%, respectively). In untreated blocks, ants were the most common cause of nest mortality followed by lack of development, displacement (primarily by the competitor *Pachodynerus nasidens*) and presumed pathogens. The invasive ant, *Ochetellus glaber* was the only observed nest predator, although the big-headed ant, *Pheidole megacephala* was also present. *Hylaeus anthracinus* inhabits coastal strand habitat which occurs in a narrow band just above the high tide line. Nests at one site were destroyed due to a high wave event, highlighting this species' vulnerability to sea level rise. Additionally, no adult bees or nests were observed at the points where yellow crazy ants, *Anoplolepis gracilipes* were established. An increased understanding of the factors limiting Hawaii's yellow-faced bees will provide information for future conservation efforts that may include landscape-scale ant control, habitat restoration and translocations.

Keywords

Anoplolepis gracilipes, *Hylaeus anthracinus*, insect conservation, invasive ants, *Ochetellus glaber*, solitary bees, yellow crazy ants

Introduction

The Hawaiian archipelago has a single group of native bees (Hymenoptera, Colletidae, *Hylaeus*), known collectively as Hawaiian yellow-faced bees. A monophyletic radiation produced at least 63 species, all of which are endemic to one or more islands in the archipelago (Magnacca 2011). Hawaiian yellow-faced bees were once one of the most abundant and widespread insect groups in the Hawaiian Islands (Perkins 1899). The group evolved with elements of the flora to form mutualistic plant/pollinator relationships (Howarth 1985; Hopper 2002; Daly and Magnacca 2003). There are few ecological studies of Hawaiian *Hylaeus* and the limited information available indicates significant declines in population and range (Magnacca 2007; Daly and Magnacca 2003; Magnacca and King 2013). In 2016, seven species received federal protection under the United States Endangered Species Act of 1973 (USFWS 2016).

Loss of both foraging and nesting habitat, competition with introduced Hymenoptera and predation by introduced arthropods may contribute to population and range reductions in Hawaiian yellow-faced bees (Hopper 2002; Lach 2008; Wilson and Holway 2010; Sahli et al. 2016; Ing and Mogren 2020). Invasive ants are thought to be a significant threat because Hawaiian yellow-faced bees, like the rest of Hawaii's endemic arthropods, are thought to have evolved in the absence of ants (Perkins 1899; Krushelnycky et al. 2005). *Hylaeus* populations may be suppressed in areas where invasive ants are present (Cole et al. 1992; Sahli et al. 2016). Invasive ants compete with *Hylaeus* bees for floral nectar and *Hylaeus* bees avoid flowers when certain ants are present (Lach 2008). The relative importance of ant predation versus resources competition on *Hylaeus* is unknown (Magnacca 2007).

Hawaiian yellow-faced bees are cavity nesters that use dead, hollow stems in vegetation or holes on the ground in soil, sand, coral rubble and under rocks (Cole et al. 1992; Magnacca 2007). They lack specialised mouthparts for excavating and are thought to be reliant on other species for initiation of holes in wooden substrates (Magnacca 2007). Females line nests with a cellophane-like, membranous material composed of lipid polymer and protein (Espelie et al. 1992). They provision cells with pollen carried in their crops and there are often multiple cells in a single nest (Daly and Coville 1982). Given the difficulty of finding and monitoring *Hylaeus* nests, very little is known about nesting ecology and factors limiting nest success. Some Hawaiian *Hylaeus* are known to use artificial wooden nest blocks (Daly and Coville 1982).

We focused on one endangered species, *Hylaeus anthracinus* (F. Smith, 1853), which primarily occurs in narrow bands of coastal habitat just above the high tide line on Oahu, Lanai, Maui, Molokai and Hawaii Island (Magnacca 2007). The species has been observed

nesting in both hollow stems and coral rubble (Graham and King 2017). No studies have attempted to estimate nesting success or describe brood number, developmental time or causes of mortality. We used artificial blocks with removable clear tubing that allowed us to unobtrusively track nest construction and development. We used a paired experimental design to evaluate the effects of invasive ants on nesting success at three sites on Oahu. We hypothesised that nests in blocks that excluded ants (i.e. treatment blocks) would have increased nesting success and produce more adults compared to nests in blocks that could be accessed by ants (i.e. control blocks). The artificial nest block design allowed us to collect additional information on nest architecture, developmental time and causes of mortality.

Study sites and methods

Study sites

Three study sites were selected, based on the presence of known *H. anthracinus* populations. Vegetation at the three sites consisted of coastal strand dominated by the native shrub *Scaevola taccada* (Gaertn.) Robx. and the introduced tree *Heliotropium foertherianum* (Hilger & Diane). Two sites [Turtle Bay (21.706075, -157.996561) and James Campbell Wildlife Refuge (JCNWR, 21.689633, -157.948752)] were on the northern coast of Oahu and one site (Ka Iwi, 21.292859, -157.660334) was on the southern shore (Figure 1). The number of monitoring points ($n = 22$) differed at the sites depending on the extent of available habitat with 15 points at JCNWR (labelled 1–15), five at Ka Iwi (labelled 16–20) and two points at Turtle Bay (labelled 21 and 22). All points were separated by a minimum of 15 metres. The two points at Turtle Bay were on a narrow peninsula, while the 15 points at JCNWR were along a long stretch of coastline (Figure 2). Based on surveys conducted in advance of nest-block deployment, the invasive black household ant [*Ochetellus glaber* (Mayr, 1862)] and the big-headed ant [*Pheidole megacephala* (Fabricius, 1793)] were present at all sites. The two species appear to partition the habitat; the twig-nesting *O. glaber* was primarily found in the vegetation, while the ground-nesting *P. megacephala* was found on the ground and was only occasionally observed foraging in the vegetation. The yellow crazy ant [*Anoplolepis gracilipes* (F. Smith, 1857)] was invading James Campbell National Wildlife Refuge from the east and the species was present at three of the 15 points at JCNWR (i.e. 13, 14 and 15). This species is ground-nesting, but was seen in high numbers foraging in the vegetation. Each of the three study sites also supported populations of invasive bees and wasps including, but not limited to, *Apis mellifera* Linnaeus, 1758 (Apidae), *Ceratina smaragdula* (Fabricius, 1787) (Apidae), *Hylaeus strenuus* (Cameron, 1897) (Colletidae), *Lasiglossum* sp. (Halictidae), *Megachile* sp. (Megachilidae) and *Pachodynerus nasidens* (Latreille 1812) (Halictidae). All Hymenoptera were initially captured and examined with a hand lens and/or microscope to observe primary characters. The Pacific Invasive Ant Key (<http://idtools.org/id/ants/pia/>) was used to identify ants and bees were identified using various taxonomic resources (Michener 2000; Daly and Magnacca 2003;

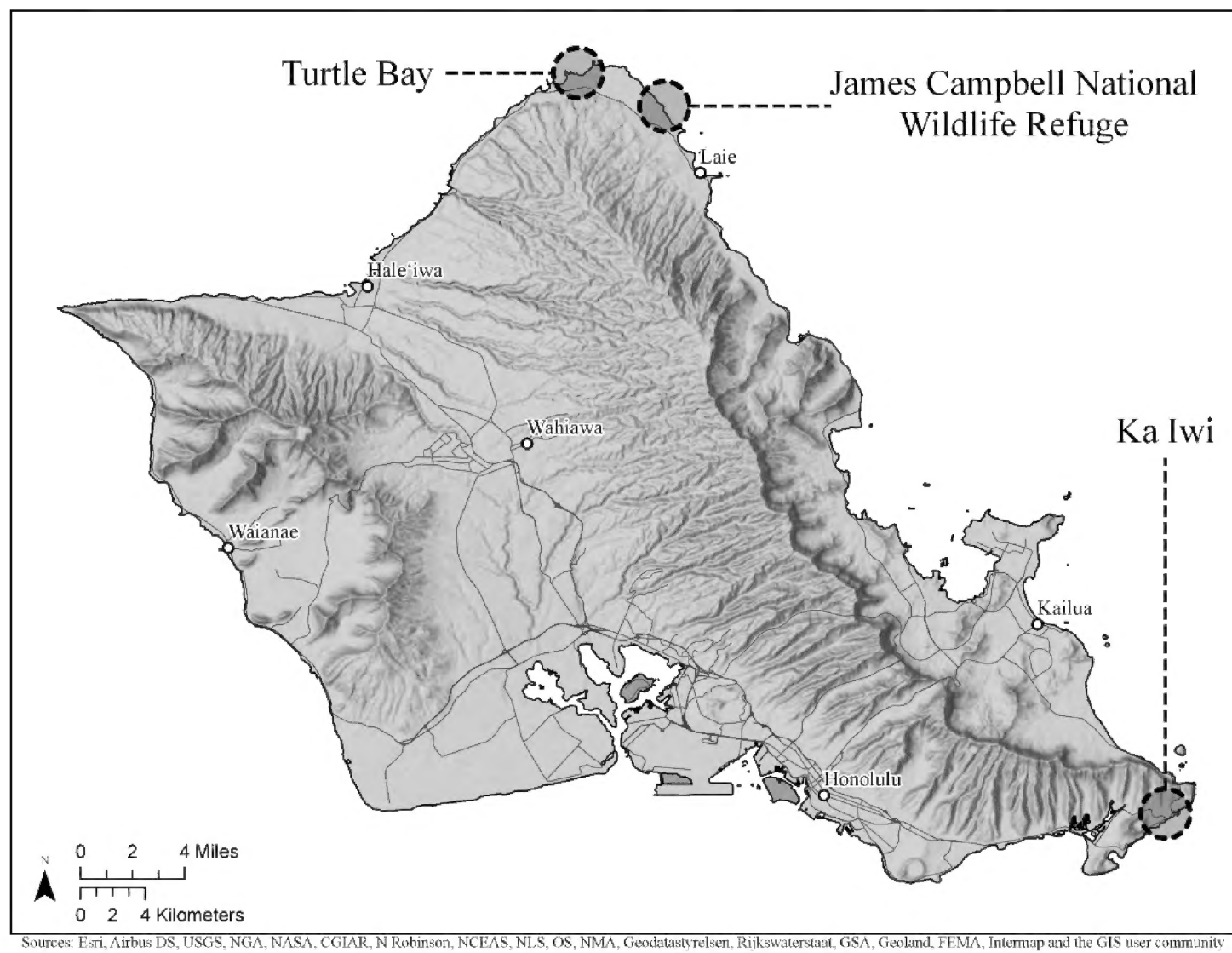


Figure 1. Three field sites, Turtle Bay, James Campbell National Wildlife Refuge and Ka Iwi (clockwise from top left) used to study the effects of invasive ants on nesting Hawaiian yellow-faced bees (*Hylaeus anthracinus*) on Oahu, Hawaii. The number of monitoring points (2, 15 and 5, respectively) varied due to extent of habitat.

Snelling 2003) and verified through comparison with existing specimens at the University of Hawaii and/or Bishop Museum Entomology collections and consultation with taxonomic experts (K. Magnacca). Specimens were deposited at the University of Hawaii Insect Museum (UHIM).

Experimental design

We used artificial nest blocks to evaluate the effects of invasive ants on *H. anthracinus* nests. Each wooden block (a section of untreated lumber 30 cm × 3.8 cm × 8.9 cm) had 20 potential nest sites, 10 on each side (Figure 3). Holes were drilled and lined with removable transparent plastic tubes creating artificial nest cavities that had an inner diameter of 4.3 mm and depth of 60 mm. This depth and diameter were based on data collected from dissections of natural nests (Graham and King 2017). The blocks were hung from vegetation using 8 mm diameter rope (Figure 4). Blocks were hung in pairs at the 22 monitoring points within two metres of each other. The rope suspending one randomly-selected block in each pair was treated with a sticky barrier



Figure 2. Coastal strand vegetation dominated by the native *Scaevola taccada* and the introduced *Heliotropium foertherianum* at James Campbell National Wildlife Refuge (JCNWR).

(Tree Tanglefoot) to prevent access by ants, while the other block remained untreated. Effort was made to ensure the blocks hung freely and were not in contact with any vegetation that would enable access by ants. We monitored blocks twice each week from December 2015 to December 2016.

During each monitoring session, the status of each potential nest site was assessed by carefully pulling out each transparent plastic tube and observing any nests. When nests were observed, we recorded the number of cells in the nest, whether a larva or pupa was present in each cell and any other relevant observations, such as discolouration or runny consistency of pollen, evidence of predation or provision raiding or the presence of moisture. Each nest was tracked over its entire development to determine its fate (i.e. the final stage reached). Nests were classified as successful if at least one adult *H. anthracinus* appeared to have emerged from the nest, failed if they did not produce at least one adult bee or unknown if the fate could not be determined.

When possible, we identified the likely cause of failure for each failed nest. Potential causes of failure included depredation by ants, lack of development (no larvae observed), presumed pathogen infection, displacement by invasive bee or wasp nests and flooding by rain or seawater. Presumed pathogen infection was based on abnormal colouration or consistency of pollen provisions and may have included fungal, bacterial



Figure 3. Treatment (left) and control (right) blocks hanging in *Scaevola taccada*. The rope suspending treatment blocks was treated with a sticky barrier (Tree Tanglefoot) to prevent invasive ants from accessing the blocks.

or viral pathogens, amongst which we did not distinguish. Although we checked nests twice a week, we undoubtedly missed some nesting attempts (i.e. bees started nests that were depredated before the next monitoring event) and we were not able to attribute outcomes to all nests. Nests in which only a back seal was observed with no pollen provisions were not counted as nests and not included in analyses.



Figure 4. Hawaiian yellow-faced bee (*Hylaeus anthracinus*) adult female and nest with three cells in plastic tubing from an artificial nest block on Oahu, Hawaii.

Data analysis

A paired t-test and a Wilcoxon signed-rank test for matched pairs were used to evaluate differences in the number of successful nests and the number of adults produced, respectively, in control vs. treatment blocks at each point ($n = 20$). All statistical tests were done using JMP Version 14 (SAS Institute Inc., Cary, NC, 1989–2020). The two Turtle Bay points were flooded during a high wave event three months into the project and were excluded from analyses because no nests produced adults in treatment or control blocks and *H. anthracinus* was no longer observed at the site through the end of the study in December 2016. The differences between the number of successful nests in control vs. treatment blocks were normally distributed (Shapiro-Wilk test: $W = 0.954$, $P = 0.43$), enabling the use of a paired t-test. We hypothesised that the mean difference between pairs of observations would be greater than zero.

We used a Wilcoxon signed-rank test for matched pairs as a non-parametric equivalent to a paired t-test to evaluate differences in number of adults produced from control vs. treatment blocks because data were not normally distributed (Shapiro-Wilk test: $W = 0.89$, $P = 0.029$). We hypothesised that the mean difference between the number of successful nests in control blocks and the number of successful nests in treatment blocks would be greater than zero.

Results

We observed a total of 961 *H. anthracinus* nests from 22 points at three study sites from December 2015 to December 2016. This included 686 nests at JCNWR, 253 nests at

Ka Iwi and 22 nests at Turtle Bay. The first sign of nest initiation was the appearance of a cellophane-like lining that sealed the back of the nest tube; this is typical in the family Colletidae. After this back lining was made, the females would deposit pollen, presumably lay an egg and then seal the chamber off and sometimes begin another cell immediately (Figure 4). The number of cells observed in a nest ranged from zero (back seal with some pollen, but no further progression) to eight with a mean of 2.59 and median of two cells. This distribution was right skewed and most nests had either one (31%) or two (23%) cells. Most nests were found after one or more cells were complete, but in 17 nests with between one and three cells, we were able to record accurate data, within 48 hours from time of nest initiation to within 48 hours of adult emergence. For those 17 nests, at least one adult emerged after an average of 37.6 days (range 29–52 days).

We were able to determine if the nest was successful or failed in 927 of the 961 nests and were able to attribute causes (i.e. successful, depredated, lack of development, pathogen, nesting by invasive wasp, flooded or adult unable to emerge) to 889 nests. In some cases when nests failed, the cause was unclear. For example, a nest may have failed due to the growth of a pathogen and was then invaded by ants. In these cases, we knew the nest failed, but were not able to attribute an outcome. In control and treatment blocks combined, 235 of the 889 (26.4%) nests produced at least one adult and the remaining 682 failed (76.7%). Of the failed nests, 654 (95.9%) could be attributed to a cause including depredated by ants ($n = 324$, 47.5%), lack of development ($n = 201$, 29.5%), pathogen ($n = 52$, 7.6%), nesting by an invasive wasp ($n = 62$, 9%), flooded ($n = 13$, 1.9%) or adult unable to emerge ($n = 2$, 0.3%) and 38 (5.6%) could not be attributed to a cause.

We found support for both of our hypotheses. Treatment blocks from which ants were excluded produced a higher number of successful nests than control blocks that could be accessed by ants (paired t-test: $t\text{-ratio} = 4.05$, $DF = 19$, $P > t = 0.0003$). The pattern was similar at individual sites, with treatment blocks having significantly higher nest success at both JCNWR (paired t-test: $t\text{-ratio} = 3.20$, $DF = 14$, $P > t = 0.0032$) and Ka Iwi (paired t-test: $t\text{-ratio} = 2.68$, $DF = 4$, $P > t = 0.0275$). In treatment blocks, 38.2% (174 of 456) of nests produced at least one adult, compared to only 14.1% (61 of 433) of nests in control blocks (Table 1, Figure 5). Not only were more nests successful in treatment blocks, but they also produced more adults compared to control blocks (11.7 ± 2.69 vs. 4.4 ± 1.15 , respectively, Wilcoxon Signed Rank: $S = 75.0$, $P = 0.0012$, Table 1, Figure 6). This pattern was also similar at both JCNWR: Wilcoxon Signed Rank: $S = 38.5$, $P = 0.01$) and Ka Iwi (Wilcoxon Signed Rank: $S = 6.5$, $P = 0.06$).

The main reason nests in control blocks failed was predation by invasive ants. Throughout the project, we observed ant predation while it was occurring in 274 instances and each time, *O. glaber* was the culprit. We found that ants invaded 70.2% (304 of the 433 nests) of the nests in control blocks (Table 1). Nests are often multi-celled and rarely ($n = 12$) ants invaded a nest, but at least one adult still emerged. Invasive ants breached treatment blocks on eight occasions: twice when treatment blocks fell to the ground due to strong winds, once when a branch was touching a treat-

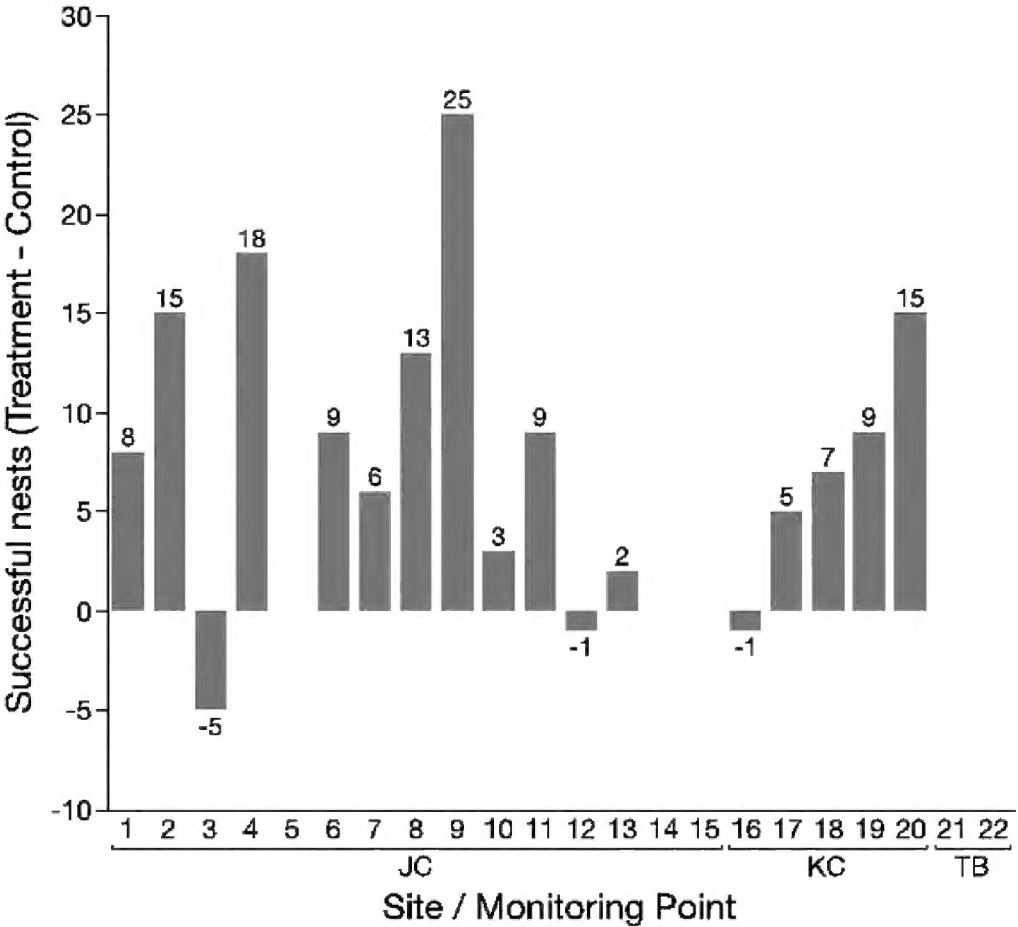


Figure 5. Difference in number of successful nests in control vs. treatment blocks at James Campbell National Wildlife Refuge (JC), Ka Iwi (KC) and Turtle Bay (TB). Numbers above zero indicate points where there were more successful nests in the treatment block (Paired t-test: t-ratio = 4.05, DF = 19, $P > t = 0.0003$). The two Turtle Bay points did not have successful nests due to flooding.

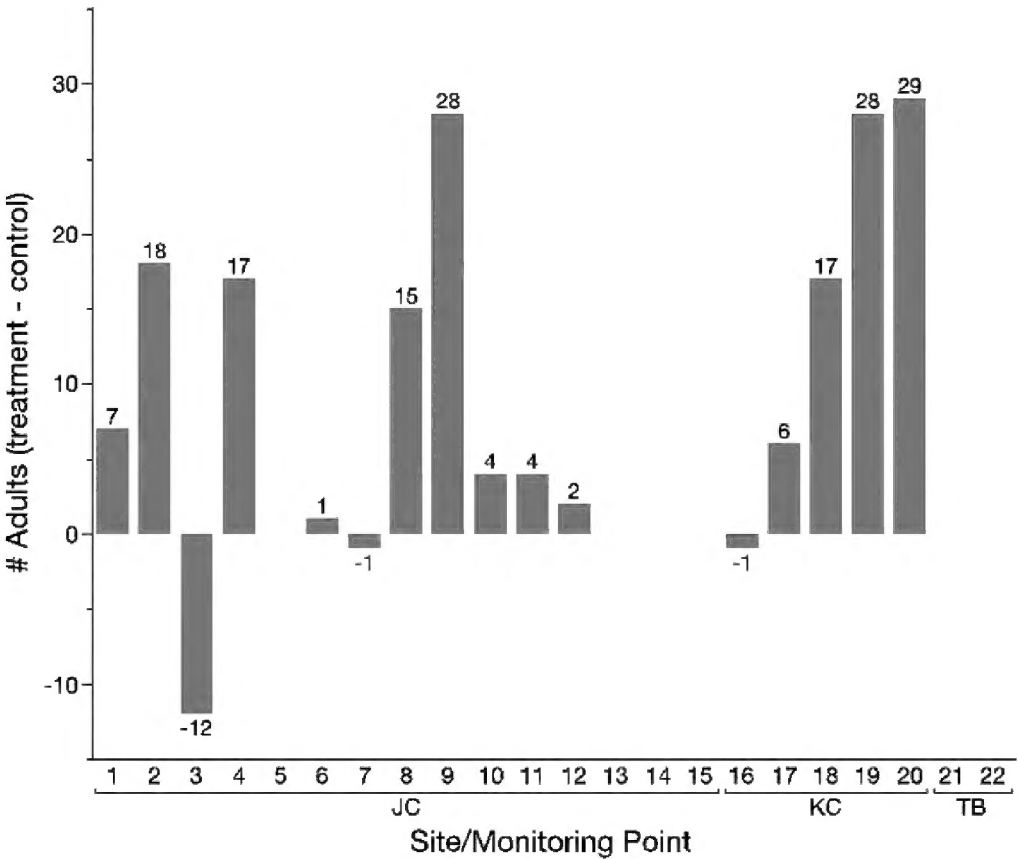


Figure 6. Difference in number of adults produced by control vs. treatment blocks at James Campbell National Wildlife Refuge (JC), Ka Iwi (KC) and Turtle Bay (TB). Numbers above zero indicate points where there were more adults produced in treatment blocks (Wilcoxon Signed Rank: $S = 75.0$, $P = 0.0012$). The two Turtle Bay points did not have successful nests due to flooding.

Table 1. Summary of control and treatment blocks invaded by invasive ants at Turtle Bay, James Campbell National Wildlife Refuge (JCNWR) and Ka Iwi on Oahu, Hawaii. The two Turtle Bay points were flooded during a high wave event three months into the project and were excluded from analyses because no nests produced adults in treatment or control blocks.

Site	Block	# points	# Successful nests	# adults produced	Mean # adults/ nest	Mean #adults/ block	# Nests invaded by ants	Total nests
Turtle Bay	Control	2	0	0	0	0	9 (64.2%)	14
Turtle Bay	Treatment	2	0	0	0	0	0	8
JCNWR	Control	15	47 (15.1%)	71	0.22	4.7	234 (75.2%)	311
JCNWR	Treatment	15	122 (37.3%)	152	0.46	10.1	10 (3.1%)	310
Ka Iwi	Control	5	14 (12.7%)	25	0.23	5	61 (56.5%)	108
Ka Iwi	Treatment	5	52 (37.7%)	104	0.75	20.8	10 (7.2%)	138
All sites	Control	22	61 (14.1%)	96	0.21	4.4	304 (70.2%)	433
All sites	Treatment	22	174 (38.2%)	256	0.54	11.6	20 (4.4%)	456

ment block, once when a block was colonised by a winged *O. glaber* queen and four times when the sticky barrier was compromised due to debris covering it. This affected 20 nests in six treatment blocks and was discovered and addressed within one to two days. The treatment block at monitoring point 3 at JCNWR was breached by ants on three different occasions causing the failure of at least three nests (Figures 5, 6).

Following predation by ants, lack of development was the second leading cause of failure in control blocks and the primary cause of failure in the treatment blocks. In control blocks, where ant predation accounted for 70.2% of failed nests, lack of development accounted for 9.9%, nesting by invasive bee or wasp accounted for 3% and the remaining two outcomes (pathogen or flooding) accounted for less than 2% each (Figure 7). In treatment blocks, nests primarily failed due to lack of development (34.6%), nesting by invasive wasps (10.7%) and then pathogens (9.9%) (Figure 7). We observed *H. anthracinus* nests being taken over by two invasive wasp or bee species: the keyhole wasp *P. nasidens* (n = 61) and leafcutter bee *Megachile* sp. (n = 1).

Between 3 December 2015 and 24 February 2016, we found 22 nests at the two points on the Turtle Bay property. All nests failed either due to predation by invasive ants (n = 9) or due to inundation (n = 13) during a large swell on 24 February 2016. As with JCNWR and Ka Iwi, only *O. glaber* was observed depredating nests. We monitored the Turtle Bay site for adults and nests through the end of the study in December 2016 and we did not observe *H. anthracinus* return; however, we did observe the invasive *H. strenuus* recolonising the site.

Discussion

Yellow-faced bee (*Hylaeus* sp.) populations in areas where invasive ants are present are known to be smaller than populations in uninvaded areas (Krushelnycky 2014; Sahli et al. 2016). In these cases, ant depredation of native *Hylaeus* nests was suspected (Cole et al. 1992), but was not documented or quantified. We found that invasive ants reduced both nest success of *H. anthracinus* and the number of adults produced per successful

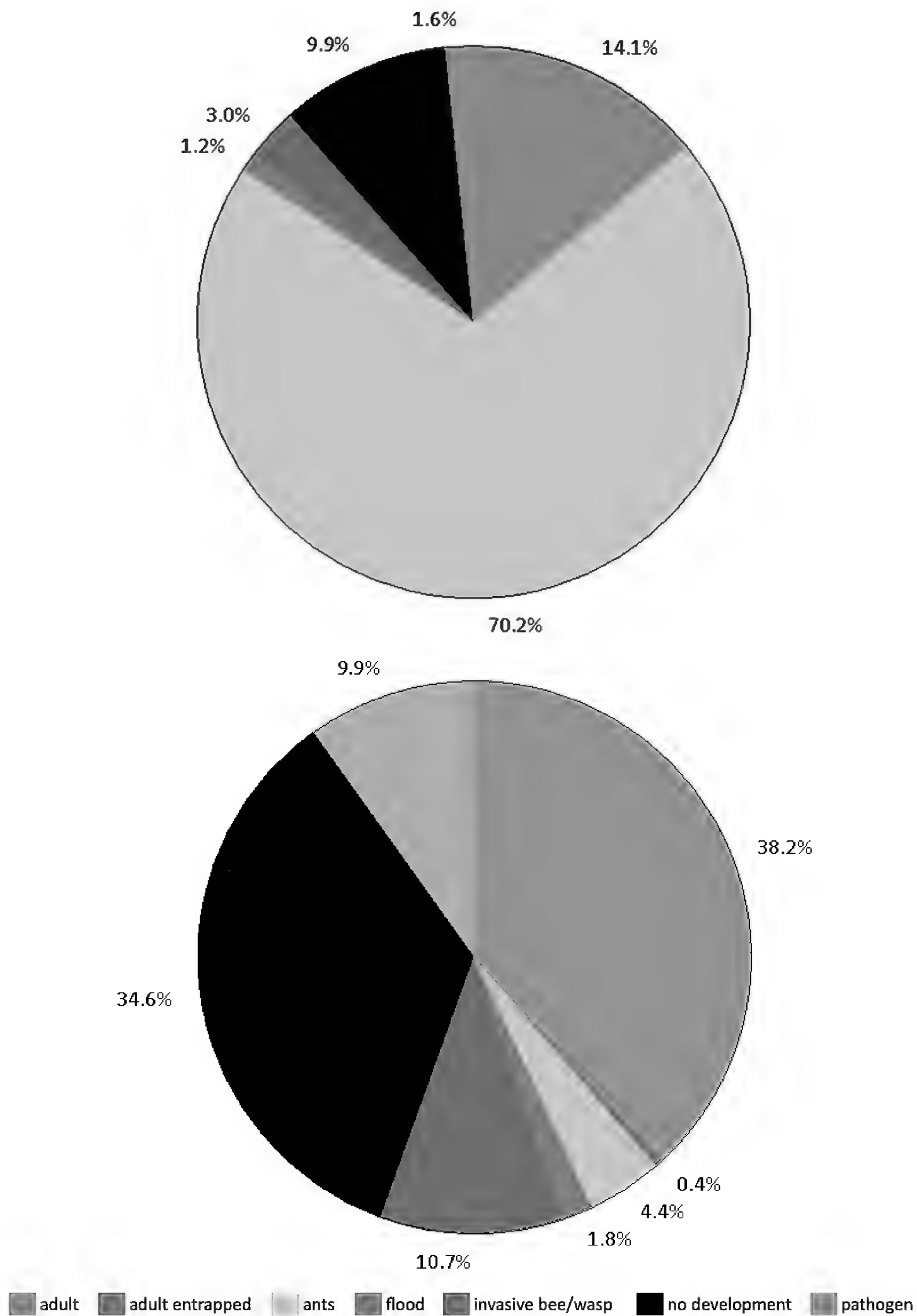


Figure 7. Nest outcomes including causes of failure in control (n = 433, top) and treatment (n = 456, bottom) blocks across the three sites (Turtle Bay, James Campbell National Wildlife Refuge and Ka Iwi) on Oahu, Hawaii.



Figure 8. *Ochetellus glaber* depredating a nest in an artificial nest block on Oahu, Hawaii.

nest. Invasive ants depredated 70.2% (304 of the 433 nests) of the nests in unprotected control blocks and were, by far, the greatest cause of nest failure (Figure 7). Nest predation by ants was substantial at all three sites, ranging from 56.5% at the Ka Iwi site to 64.2% at Turtle Bay and 75.2% at JCNWR (Table 1).

In the areas where *P. megacephala* and *O. glaber* were the dominant ant species, *O. glaber* was regularly seen forming recruiting lines into nests and removing the contents including pollen, eggs, larvae and pupae (Figure 8). In all instances where depredation by ants was observed ($n = 274$), *O. glaber* was the culprit, even though *P. megacephala* was common at all sites. The two species seemed to segregate into different niches, with *P. megacephala* more commonly observed on the ground while *O. glaber*



Figure 9. Yellow crazy ant (*Anoplolepis gracilipes*) investigating a nest tube in one of the nesting blocks on Oahu, Hawaii.

was primarily observed in the vegetation. The only observation of *P. megacephala* depredating a nest tube occurred on 11 September 2016 at JCNWR and it did not involve a nest of *H. anthracinus*. In that instance, we observed more than 100 *P. megacephala* depredating a nest of an unidentified wasp filled with paralysed spiders. However, we did observe a *P. megacephala* worker attempting to enter a *H. anthracinus* nest in a tube we had temporarily removed from a block and placed on a fence post. In this case, the adult female bee was blocking entrance to the nest and prevented the ant from accessing the nest. We commonly observed females in nests during nest construction, but rarely after construction was completed, thus nests are unattended throughout most of their development.

Hawaiian yellow-faced bees are known to nest in dead, hollow stems or holes on the ground in soil, sand, coral rubble and under rocks (Cole et al. 1992; Magnacca 2007; Magnacca 2020). We saw large numbers of *H. anthracinus* nesting in the coral rubble just above the high tide line at the Ka Iwi site. We did not observe this at our other sites. One possible explanation for persistence of ground nests at Ka Iwi is the lower populations of *P. megacephala* along the coastline at Ka Iwi. We did not measure ant densities at each site, but we often noted seeing fewer ants on the ground in the coral rubble area at Ka Iwi compared to our other sites. Although *H. anthracinus* can co-exist with *P. megacephala* at some density (Magnacca and King

2013), *P. megacephala* may play an important role in excluding them from ground nesting. Since our study used nest blocks hanging in shrubs, it did not evaluate the impact of ants on ground nesting.

While *H. anthracinus* populations may be able to persist with *O. glaber* and *P. megacephala*, we found no evidence that it can co-exist with the yellow crazy ant (*A. gracilipes*). *Anoplolepis gracilipes* was invading JCNWR from the east and was present in high densities at two points (14 and 15) and at low densities at point 13 at the beginning of our study (Figure 9). Although the vegetation structure and plant species composition was similar at these three points, *H. anthracinus* adults were not observed in the area and no nests were found at points 14 and 15 and only two nests were found in the treatment block at point 13 over the course of the year-long study (Figure 5). By the end of our study, the range of *A. gracilipes* had expanded and the species was also present in low densities at points 11 and 12. This amounts to an expansion of approximately 60 m in one year and represents a significant threat to the long-term persistence of *H. anthracinus* at this site.

Hylaeus anthracinus appeared to have few defences against invasive ants. One type of behaviour we observed that may be beneficial in deterring ants involved the female adult bee remaining stationary at the entrance of the nest facing outwards. It is unclear if adult bees seen exhibiting this behaviour are simply resting or actively guarding the nest from kleptoparasites or other parasites or predators. Regardless of its origins, we observed this behaviour preventing ants from accessing nests on several occasions. However, female bees were typically observed in their nests only during active construction. Once all nest cells were completed and sealed, the bees were no longer present, leaving nests vulnerable to ant predation during brood development.

Our study design and monitoring methods had weaknesses. Although we monitored the nest boxes twice a week for a year, some bee nests were initiated and depredated in between visits, so it is possible the number of failed nests and those depredated by ants is an underestimate. Alternatively, it is possible that our estimate of nest predation by ants is higher than that which occurs in a natural setting. As outlined in the Methods section, our wooden blocks had 20 pre-drilled holes, 10 on each side. In control blocks, it is possible that, once invasive ants found the block, they were more likely to depredate all nests present in the block. This contrasts to natural conditions where nests are distributed in hollow stems across a host plant and are likely to be further apart and require additional foraging effort on the part of the ants. Similarly, the structure of the nest blocks may have increased the likelihood of invasive competitors easily utilising the available nest holes and/or of pathogens spreading quickly between nests. Additionally, nests in treatment blocks appeared to fail at a higher rate due to lack of development (34.5%) than nests in control blocks (9.9%). We surmise that high levels of predation by ants in control blocks across all available nests may mask what would otherwise be higher numbers of nest failures due to lack of development. The seemingly high number of nests that failed to develop may have been associated with elevated levels of moisture in the plastic tubing used in our artificial nests, although we lack data from natural nests for comparison. A comparison of nest success

rates in a variety of artificial nest materials, including more porous or breathable tubes, would be valuable.

While this study was not designed to evaluate other threats to *H. anthracinus*, the loss of all surviving nests ($n = 13$) and apparently the entire population, on the peninsula at Turtle Bay due to inundation during the large swell on 24 February 2016 illustrates and documents their vulnerability to storms, large swell events and sea-level rise compared to most species. Although this species was widespread historically (Perkins 1899), currently, *H. anthracinus* is only observed in the narrow strip of coastal strand vegetation above the high tide line on Oahu. Populations are unlikely to move inland as sea-level rises because of development and the presence of degraded habitat dominated by invasive species. A study using high-resolution dynamic model experiments found an increased frequency of tropical cyclones from 1980 to 2018 over the Central Pacific (i.e. the area around Hawaii and extending east and south) that could only be explained by factoring in human-accelerated climate change (Murakami et al. 2020). Based on this, we expect continued increased storm frequency in the Central Pacific. The coastal flooding and erosion that accompany these storms could be detrimental to *H. anthracinus* populations.

The lowland arthropod fauna of Hawaii has been largely eclipsed by non-native species and less than 5% of arthropod species in coastal areas on Oahu are native (Plentovich 2010). Invasive ants, bees and wasps (e.g. *A. mellifera*, *C. smaragdula*, *C. dentipes*, *Lassioglossum* sp., *H. strenuus* and *P. nasidans*) now dominate pollinator webs in coastal areas of the Hawaiian Islands (Hopper 2002; Shay et al 2016; Shell et al. 2017; Shay and Drake 2018). Not only do these invasive pollinators compete with *H. anthracinus* for floral resources (Lach 2008; Ing and Mogren 2020), but they may also compete for nest sites. Introduced pollinators have been found to utilise the same plants and similar dimensions for nest cavities in wild nests (Graham and King 2017). We observed three invasive hymenopteran species nesting in our artificial nest boxes: *P. nasidans*, *Megachile* sp. and *H. strenuus*. Cumulative impacts of such nest site competition are unknown; however, it is reasonable to assume that the presence of these invasive competitors places additional stresses on coastal-dwelling endangered yellow-faced bees, like *H. anthracinus*.

Conclusion

Once widespread, most species of Hawaiian yellow-faced bees are now extremely rare and, given their small size and cryptic nature, very little is known about their nesting ecology, including factors limiting nest success. *Hylaeus anthracinus* is one of a limited number of native terrestrial invertebrates persisting in coastal areas of the main Hawaiian Islands, but its populations are sparse and patchily distributed. We found that invasive ants had a severe to catastrophic effect on nesting *H. anthracinus*, depending on the ant species present. In our study, the invasive ant *O. glaber* depredated the majority (70%) of bee nests built in unprotected nest blocks. In areas invaded and with high densities of yellow crazy ant (*A. gracilipes*), no nests were initiated and no adult

bees were observed, suggesting that invasion by these ants may completely exclude *H. anthracinus*. The compounding effects of predation by invasive ants, habitat loss and resource competition with invasive Hymenoptera are unknown, but all are likely to have contributed to the decline of *H. anthracinus*. The few remaining *H. anthracinus* populations on Oahu are constrained to a narrow strand of coastal habitat just above the high tide line, making the species vulnerable to sea level rise and increased storm frequency and intensity, both of which are predicted as the climate changes.

Hawaiian yellow-faced bees evolved with elements of the flora to form mutualistic plant/pollinator relationships (Howarth 1985; Hopper 2002; Daly and Magnacca 2003). Without the onset of active management for this species, we expect populations to further decline as invasive ants, especially yellow crazy ants, continue to expand their distribution (Chen 2008). Ecological restoration of coastal ecosystems in Hawaii is necessary to improve and expand habitat for Hawaiian yellow-faced bees and other native invertebrates in support of existing plant/pollinator relationships. Safe and effective ant control and/or eradication methods as part of habitat restoration are needed to allow the recovery of Hawaiian yellow-faced bees. Additional testing of novel control technologies like RNA interference, *Wolbachia*-based approaches and improved delivery methods for toxicant baits are needed to control invasive ants at a landscape scale. Once suitable habitat is identified or areas are restored, translocation could be used to expand the range of this and other Hawaiian yellow-faced bees.

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